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Noise-induced spatial dynamics in the presence of memory loss

Matjaž Perc*, Marko Marhl

Department of Physics, Faculty of Education, University of Maribor, Koroška cesta 160, SI-2000 Maribor, Slovenia

Abstract

We study the spatial dynamics of noise-induced waves in two-dimensional excitable media in dependence on the duration of the artificially imposed refractory time that is introduced to each constitutive system unit after an excitation. Due to the introduction of refractory times, a randomly induced spatial wave is temporarily unable to transmit information to the opposite site of its propagation direction. Thus, once the wave leaves the absorbing boundaries of the spatial grid the system has little or no recollection, depending on the duration of the refractory time, of its existence. We show that even in the presence of such memory loss, self-organization of excitatory events leads to noise-induced spatial periodicity in the media. We present a simple analytical treatment of a two-unit system to capture and explain the essence of the observed phenomenon. Since refractory times are widespread in biological systems, our results provide interesting insights into functioning of real-life organisms at the cellular as well as tissue level.

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1. Introduction

During the last decade noise-induced phenomena in spatially extended systems [1] have attracted considerable attention in the scientific community. In two-dimensional excitable media spatiotemporal stochastic resonance was first reported in Ref. [2]. Particularly, authors of Ref. [2] have shown that spatiotemporal correlations with an excitatory wave, determined by the time averaged number of excess events, exhibit a resonant dependence on the intensity of noise that is introduced to the medium consisting of noisy threshold devices. Related phenomena, such as noise controlled spiral growth in excitable media [3], noise sustained waves in subexcitable media [4], or noise induced or enhanced spatiotemporal order in general, were subsequently reported also for real-life-based models, like the medium consisting of FitzHugh–Nagumo excitable neurons [5], or the photosensitive Belousov–Zhabotinsky chemical medium [6,7]. Moreover, authors of Ref. [8] adopted an innovative approach by studying the impact of parametric noise on the spatiotemporal dynamics of a cellular automaton subexcitable medium. They have discovered that intermediate noise intensities support the existence of pulsating spots, while larger levels of parametric noise yield a collective

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*Corresponding author. Tel.: +386 2 2293643; fax: +386 2 2518180.

E-mail address: matjaz.perc@uni-mb.si (M. Perc).

URL: http://fizika.tk/.

state in which all units of the medium fire synchronously [8]. Noteworthy, while in the past, the majority of studies considered only spatially and temporally white noise, recently, the influence of spatiotemporally correlated noise on structure formation in excitable media has also been studied thoroughly [9]. Apart from above-summarized studies reporting rather mainstream noise-induced spatiotemporal order in nonlinear media, there also exist very interesting literature reporting noise sustained coherence of space–time clusters and self-organized criticality [10], noise-enhanced and induced excitability [11,12], noise-induced propagation of harmonic signals [13], noise-promoted cooperation [14], as well as noise-sustained and controlled synchronization [15] in spatially extended systems.

More recently, specifically the spatial dynamics of noise-induced excitatory events in spatially extended systems has been investigated in great detail. Carrillo et al. [16] clearly emphasized and distinguished the difference between spatiotemporal and spatial order in spatially extended systems. While spatiotemporally ordered behaviour can be quantified in many ways, using for example the time-averaged number of excess events at the position of the travelling wave [2] or spatial cross-correlation and mutual information measures [9], spatial order can be explicitly quantified by the spatial structure function [1,16]. Authors of Ref. [16] have shown that, for a nonlinear media near a pattern-forming instability, there exist an intermediate value of additive spatiotemporal noise for which the peak of the circularly averaged spatial structure function is best resolved, thus marking spatial coherence resonance in the system. A conceptually identical phenomenon was subsequently reported also for excitable media in Ref. [17]. Moreover, the noise-induced spatial dynamics of excitable media was also studied in dependence on subthreshold travelling waves of various widths and shapes in order to shed light on the possibility of spatial stochastic resonance [18].

To stress the difference between spatial and temporal or spatiotemporal dynamics of nonlinear media even more thoroughly, we recently studied also effects of small-world connectivity [19,20] on the spatial dynamics of two-dimensional media. In contrast with studies reporting a constructive effect of small-world connectivity on the temporal or spatiotemporal dynamics of one-dimensional networks, assuring for example self-sustained activity [21] and fast coherent responses [22] or amplification of stochastic [23] and coherence [24] resonance in the system, we showed [25] that in fact small-world connectivity impairs or even totally destroies noise-induced spatial order in excitable media already by a very small fraction of introduced shortcut links.

In the present paper, we study another important aspect of noise-induced spatial dynamics in excitable media that is brought about by introducing a refractory time after each excitation of a particular constitutive system unit. Due to the introduction of the refractory time, noise-induced excitatory waves cannot influence those spatial units that are on the opposite site of the propagation direction of the wave. Thus, once the wave leaves the absorbing boundaries of the spatial grid the system has little or no recollection of its existence. In particular, if the refractory time is longer than the wave needs to disappear through the absorbing boundaries of the spatial grid the memory loss is complete. We show that even under such conditions, self-organization of excitatory events leads to noise-induced spatial periodicity in the media that is resonantly pronounced for some intermediate level of additive spatiotemporal noise. To demonstrate this novel type of noise-induced transition to spatial order we use a simple one-dimensional excitable system with a piece-wise linear periodic potential as the constitutive unit of the two-dimensional excitable media. Importantly, due to the simplicity of the model, the refractory time of each constitutive unit can be judiciously adjusted via a single parameter, and the spatially extended system can be traced analytically. Specifically, we succeed in explicitly linking the resonant noise induced spatial frequency with the duration of the refractory time.

Although authors of Ref. [2] introduce a refractory time for the noisy threshold devices constituting the excitable medium, they do not study the role of different refractory times in much detail. Moreover, in Ref. [8] the refractory time of the cellular automaton subexcitable model is no longer considered a constant parameter as in Ref. [2], but is determined by the dynamics of the system itself. Beyond that, however, we were unable to find literature studying the impact of different refractory times on the noise-induced order in two-dimensional nonlinear media. Thus, the present work appears to be the first to systematically analyse the effects of different refractory times on the noise-induced spatial order in excitable media, specifically by considering the refractory time as the key system parameter. Thereby, the use of the presently applied simple one-dimensional excitable system with a piece-wise linear periodic potential as the constitutive unit of the two-dimensional excitable media is crucial, since it enables precise variations of the duration of the refractory time. Note that this is usually not the case even when considering fairly simple real-life-based models, such as for example the

FitzHugh–Nagumo or Belousov–Zhabotinsky nonlinear medium, where the refractory time of each unit often depends on several system parameters in an entangled nonlinear fashion.

We emphasize that refractory times after excitatory events are very common in real-life biological systems. Examples range from the human heart to the intra- and inter-cellular signalization, thus encompassing the cellular as well as tissue level. From the physical point of view, the introduction of refractory times enables a systematic analysis of differences between the noise-induced spatial dynamics of nonlinear media that is locally modelled by excitable nodes and the one modelled by excitable focuses. Note that stable excitable foci can have a very long re-settlement phase after an excitation, during which they are virtually immune to external influences such as noise or deterministic signals. Thus, the present study is interesting both from the applicative biological as well as the physical point of view.

The paper is structured as follows. Section 2 is devoted to the description of the mathematical model while Section 3 features the analysis of the noise-induced spatial dynamics. In the last Section we summarize the results and outline biological implications of our findings.

2. Mathematical model

As the constitutive unit of the spatially extended system, we presently use a simple one-dimensional model with a doubly piece-wise linear periodic potential given by

$$\frac{du}{dt} = f(u) = (1 - a)\Theta(u_c - u) + b\Theta(u - u_c), \tag{1}$$

where $0 \leqslant u \leqslant 2\pi$ is the phase of the system, Θ is the Heaviside function, $u_c > 0$ is the firing threshold, whilst parameters $a > 1$ and $b > 0$ determine the kinetics of the system for $u < u_c$ and $u > u_c$, respectively. More precisely, the parameters a and b determine the velocity of changes of u, which is given by $f(u)$. As shown in Fig. 1, for $u < u_c$ the velocity is $f(u) = 1 - a$, whereas for $u > u_c$ we have $f(u) = b$. Notably, the same model has already been used previously by Pradines et al. [26] to study the essential role of slow and fast dynamics for constructive effects of noise on the temporal dynamics of the system. For the above parameter values the system has a single excitable steady state at $u = 0$. Small perturbations of $u = 0$ evoke large-amplitude spikes ($u = 2\pi$) if u is forced to exceed u_c.

Importantly, by setting $b \gg (a - 1)$ the model given by Eq. (1) quickly re-occupies the steady state after each excitation and is thus virtually instantly ready to get excited again by the same weak perturbation that evoked the preceding excitation. Hence, $u = 0$ acts as an excitable steady node. This mathematical concept is, however, at odds with several real-life situations where an excitation cannot be immediately followed by the
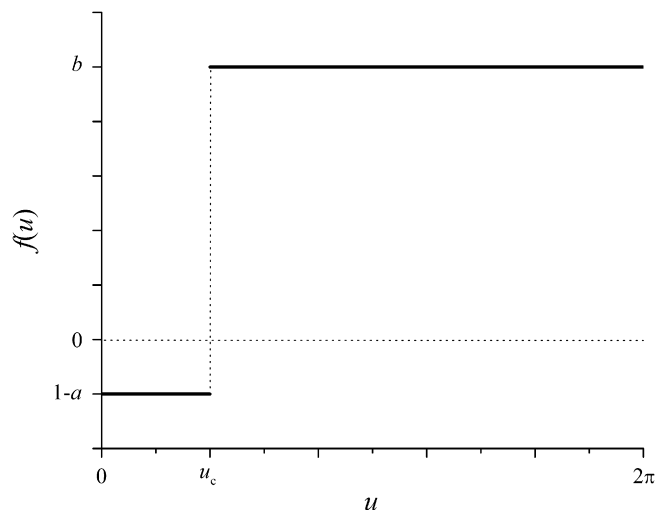

Fig. 1. The system dynamics is determined by the velocity of changes of u, i.e. $f(u)$, which is determined by parameters $a > 1$ and $b > 0$. The velocity is $f(u) = 1 - a$ for $u < u_c$, and $f(u) = b$ for $u > u_c$.

next. To account for this fact we introduce a refractory time t_r that sets in after each excitation $u = 2\pi$. During t_r we set $u \equiv 0$ independent of the external forcing. This alteration of Eq. (1) can have wide-reaching effects on the noise-induced spatial dynamics of the nonlinear media that is formally given by

$$\frac{du_{ij}}{dt} = f(u_{ij}) + D\nabla^2 u_{ij} + \xi_{ij}(t),$$ (2)

where u_{ij} is considered as a dimensionless two-dimensional scalar field on a discrete $n \times n$ square lattice with mesh size $\Delta x = 1$. $\xi_{ij}(t)$ is temporally white Gaussian noise with zero mean satisfying the spatial correlation $\langle \xi_{ij} \xi_{op} \rangle = \sigma^2 \delta_{io} \delta_{jp} / \Delta x^2$, where $\sigma / \Delta x$ is the standard deviation of a temporally and spatially white noise in a discrete space [1]. The Laplacian $D\nabla^2 u_{ij}$, D being the spatial coupling constant, is incorporated into the numerical scheme via a five-point finite-difference formula as described by Barkley [27], using absorbing boundary conditions. The whole system is integrated numerically with the Heun method [1] using $dt = 0.002$.

3. Noise-induced spatial dynamics

In what follows, we will analyse effects of different t_r on the noise-induced spatial dynamics of the excitable media under study. System parameters used in subsequent calculations are: $a = 1.05$, $b = 8.0$, $u_c = \pi/30$, $D = 0.32$, and $n = 128$. Moreover, the system is initiated from steady-state excitable conditions $u_{ij} = 0$ for $\forall i$, j, and the standard deviation of Gaussian noise is adjusted so as to induce the most coherent spatial dynamics in the system. By calculating the spatial structure function [16] for different levels of additive noise, we find that for the above system parameter values $\sigma = 0.04$ yields the most ordered spatial patterns independent of t_r.

We start by examining the evolution of noise-induced spatial periodicity by $t_r = 0$ shown in Fig. 2. At the beginning, we can observe first excitations that appear randomly in the array. These excitations represent epicentres for the waves that then propagate across the spatial grid. Importantly, as the initial wave front propagates across the array it excites units in its path as well as the ones in the interior of the circular wave, thus yielding a continuous series of excited and quiescent circularly shaped stripes that alternate periodically across the entire space.

Although nearly identical at first, the evolution of spatial dynamics by $t_r = 1.8$ shown in Fig. 3 appears rather different. Similarly as by $t_r = 0$, the initial stage is characterized by localized epicentres formed by excited spatial units, which represent seeds for the emerging waves. However, due to the refractory time there is no information transfer in the opposite side of the propagation direction of the waves. Note that every excitation is followed by a quiescent phase and the unit has to wait for time t_r before it can be excited again irrespective of the strength of external perturbations. Thus, a memory loss sets in since the system gradually loses recollection of the initial state. In particular, if t_r is large enough the wave may reach the absorbing boundaries of the system and hence the memory loss is complete. It is unlikely to expect spatial periodicity
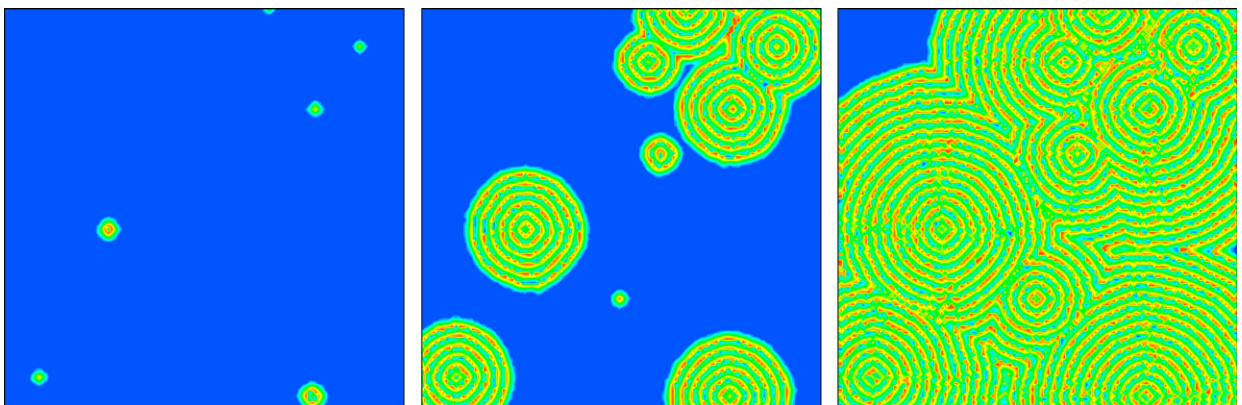

Fig. 2. Characteristic snapshots of the spatial profile of u in the absence of memory loss ($t_r = 0$) at different times ($t = 3.2$; 6.8; 16.4) increasing from the left towards the right panel. All figures are depicted on 128×128 square grid with a linear colour profile, red marking 2π and blue 0.0 values of u.
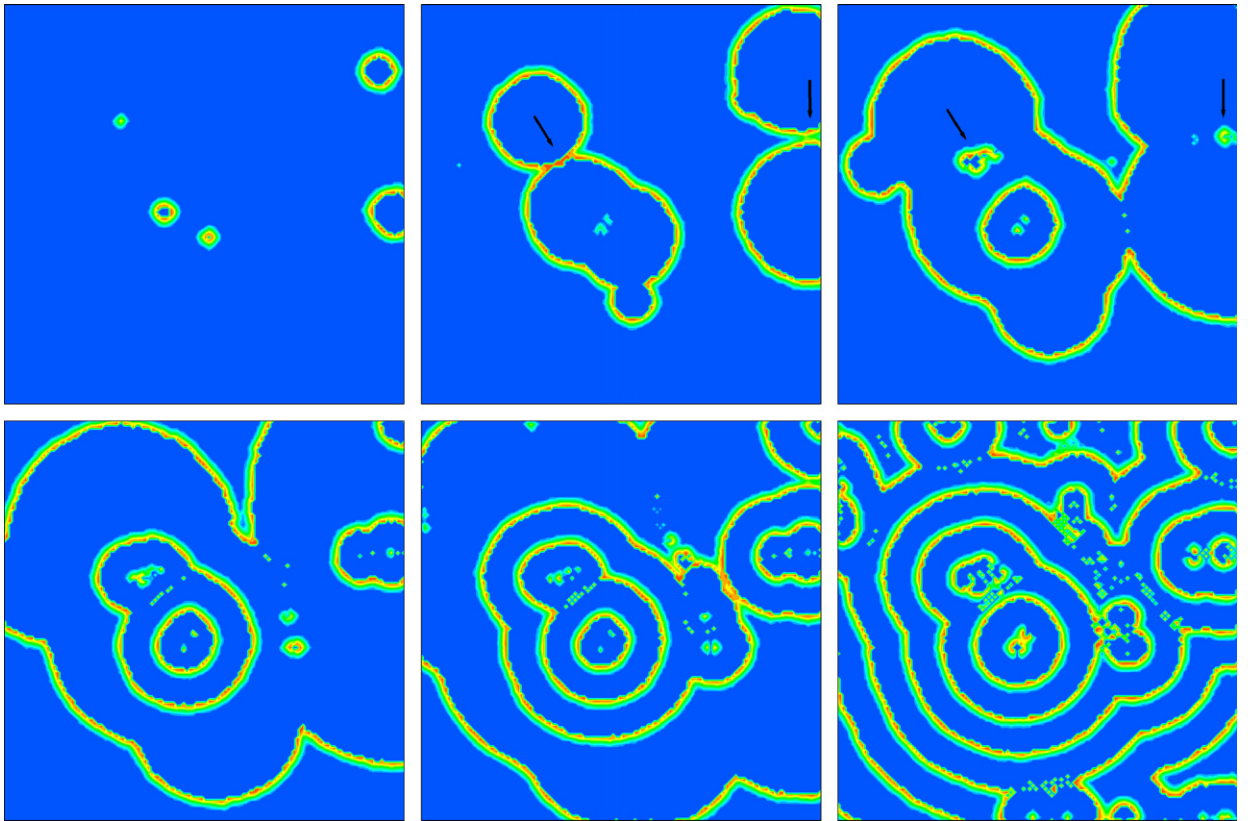
Fig. 3. Characteristic snapshots of the spatial profile of u in the presence of memory loss ($t_r = 1.8$) at different times ($t = 3.4$; 7.2; 10.2; 13.0; 15.8; 23.0) increasing from the top left towards the bottom right panel. All figures are depicted on 128×128 square grid with a linear colour profile, red marking 2π and blue 0.0 values of u.

emerging under such conditions. Remarkably though, we argue that places where two wave fronts of different origin collide (arrows in the top middle panel) hold promise of recovering the seemingly lost spatial periodicity due to the subsequent emergence of clusters (arrows in the top right panel) that act as new epicentres for excitatory waves. It is crucial to note that due to the interference phenomenon in the cluster not all of the units get excited simultaneously; however, many of them are very near the spiking threshold and can thus be considered as super-excitable units. These so-called super-excitable units are highly susceptible to noise, and that is why each cluster is seeded with excitations irregularly appearing as puffs in its interior. It is also very important that the cluster consists of a large enough number of coupled units, since only large clusters can remain active for a long enough time in comparison with the refractory time t_r. The long life span of large clusters is crucial because a potential wave can emerge from a cluster only after the surrounding units have finished their quiescent phase. The above-outlined scenario thus indicates that the spatial frequency of the waves depends strongly on t_r. The bottom row of Fig. 3 shows how the spatial waves develop further in time and form a periodic spatial pattern, thus supporting validity of our reasoning.

To quantify spatial periodicity of noise-induced patterns in Figs. 2 and 3 precisely, we calculate the circularly averaged spatial structure function

$$s(k) = \int_{\Omega_k} S(\vec{k}) \mathrm{d}\Omega_k, \qquad (3)$$

where $\vec{k} = (k_x, k_y)$, Ω_k is a circular shell of radius $k = |\vec{k}|$, and $S(k_x, k_y) = \langle H^2(k_x, k_y) \rangle$ is the spatial structure function calculated on the basis of the spatial Fourier transform $H(k_x, k_y)$ of the u field. Results are presented in Fig. 4. It can be observed that for $t_r = 0$ and $t_r = 1.8$ there exists a particular spatial frequency marked with a dashed line at $k = k_a$ and dotted line at $k = k_b$, respectively, that is well pronounced in both cases.
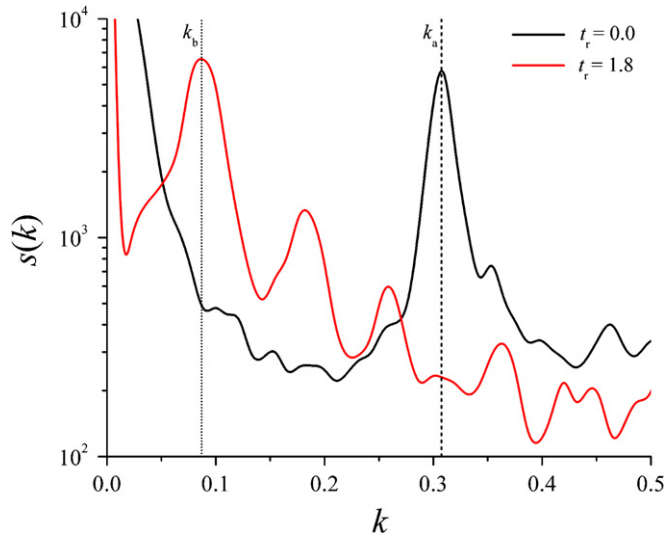
Fig. 4. Circular average of the spatial structure function for two different values of t_r corresponding to the spatial profiles in Figs. 2 and 3.

Importantly, note that k_a and k_b differ substantially (by a factor of 3.5). Thus, results in Fig. 4 fully support above visually assessed findings, implying the fact that additive spatiotemporal Gaussian noise of appropriate intensity can evoke spatially periodic patterns even in the presence of memory loss, whereby the spatial frequency k of noise-induced patterns depends heavily on the value of t_r.

In the following, we will show that the function $k(t_r)$ can be estimated analytically. The key enabling the derivation of $k(t_r)$ is to understand wave propagation in an array of excitable units. The propagation of a wave front depends on how fast an excited unit can activate its quiescent neighbouring unit, i.e. on the activation time t_a, which is defined as the time a quiescent unit needs to reach the firing threshold $u = u_c$. In case of periodic waves, as shown in the last panels of Figs. 2 and 3, the next wave front always appears after an integer multiple of t_a. In particular, the wavelength $\lambda = 1/k$, representing the distance between two neighbouring wave fronts, depends on the number of sequential excitations that appear during one full oscillation period t_0 (time between two consecutive spikes). Thus, λ is determined by

$$\lambda = \frac{t_0}{t_a} \Delta x, \tag{4}$$

where Δx is the size of a single unit. t_0 is the sum of the activation time t_a, the excursion time t_e (width of each spike), and the refractory time t_r, i.e. $t_0 = t_a + t_e + t_r$. Since in Eq. (1) $b \gg a - 1$ and $u_c \ll 2\pi$, the excursion time can be estimated by $t_e \approx 2\pi/b$. By taking $\Delta x = 1$, we can write Eq. (4) in the following from:

$$\lambda \approx \frac{2\pi + b(t_a + t_r)}{b t_a}. \tag{5}$$

Evidently, in order to obtain the desired function $\lambda(t_r)$ [and hence $k(t_r)$], we have to estimate the activation time t_a, which is the time in which an excited unit is able to force its neighbouring quiescent unit from its steady state at $u = 0$ to the threshold value $u = u_c$. Thereby, the excited unit has to overcome the internal resistance of the quiescent unit given by $du/dt = 1 - a$, which imposes a tendency towards $u = 0$. The dynamics of the excited neighbour is determined by the fast kinetics $du/dt = b$. Since $u_c \ll 2\pi$ the excited variable changes practically as $u = bt$. Thus, the dynamics of a quiescent unit, coupled with an already excited unit, can be described by the equation

$$\frac{du}{dt} = 1 - a + D(bt - u). \tag{6}$$

Integrating Eq. (6) for the initial condition $u|_{t=0} = 0$ gives an implicit equation for t_a that reads
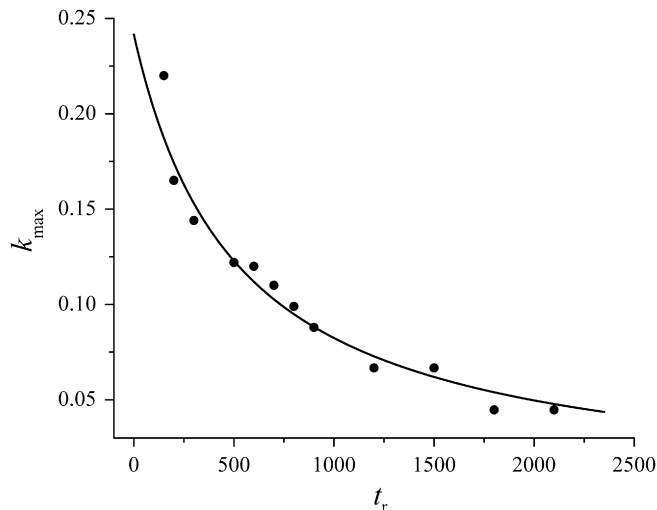
$$c e^{-D t_a} + b t_a = u_c + c, \tag{7}$$

Fig. 5. Dependence of the resonantly enhanced spatial wave number k_{max}, corresponding to the first maximum of $s(k)$, on different values of t_r. Symbols indicate numerically obtained values, whilst the solid line shows the derived analytical dependence given by Eq. (9).

where $c = (a + b - 1)/D$. In order to obtain an explicit expression we simplify Eq. (7) by applying the approximation $e^{-Dt_a} \approx 1 - Dt_a + D^2 t_a^2/2$. By retaining the physically relevant positive solution and considering that $b \gg a - 1$, we obtain

$$t_a \approx \frac{a - 1 + \sqrt{2bDu_c}}{bD}. \tag{8}$$

By inserting the expression for t_a into Eq. (5), we find that the spatial frequency $k = 1/\lambda$ can be estimated according to

$$k(t_r) \approx \frac{a - 1 + \sqrt{2bDu_c}}{2\pi D + bDt_r + a - 1 + \sqrt{2bDu_c}}. \tag{9}$$

To evaluate the accuracy of Eq. (9), we compare analytical predictions with the values resulting from the numerical integration of Eq. (2). However, since the above analytical treatment was conducted without taking into account noise (note that we have just assumed that one unit is excited and the other completely quiescent), we first have to take into account non-zero values of σ. We do this simply by acknowledging the fact that the non-zero σ decreases the effective threshold value of each spatial unit. Thus, when integrating Eq. (6) the initial state of variable u is not exactly zero, but in fact $u|_{t=0} = \varepsilon > 0$. We found that, for the presently applied $\sigma = 0.04$, on average $\varepsilon = 0.35u_c$. This has nearly the same effect as if u_c in Eq. (9) is replaced by the effective threshold $0.65u_c$, which is also the value we have used for evaluating the results presented in Fig. 5. It is evident that the analytically predicted values of the resonantly enhanced $k = k_{max}$ obtained with Eq. (9) are in good agreement with the numerically calculated values, thus validating our above arguments and treatment.

4. Summary and discussion

We study effects of memory loss on the noise-induced spatial dynamics of excitable media. The introduction of refractory times limits the information transfer in the media only to those spatial directions that are equal to the spreading direction of excitatory waves, thus effectively introducing an information transmission barrier in the system. We show that despite the potentially imposed memory loss occurring by long refractory times, the system is still able to self-organize into a spatially coherent dynamical state that is characterized by a well-defined spectral peak of the circularly averaged spatial structure function. Due to the minimalist nature of the studied system the noise-induced spatial dynamics can be traced analytically via a simple treatment of a two-unit system, thus explaining the essence of the observed phenomenon.

We argue that the introduction of refractory times enables a systematic analysis of non-linear media whose units are modelled by excitable focuses rather than nodes [17]. This is an important distinction since stable focuses are often characterized by long re-settlement times during which they are extremely robust against external influences, as indicated by the very negative local divergence during that period [28,29]. On the contrary, stable nodes regain full excitability immediately after an excursion. In this sense, the introduced refractory times model the noise robust re-settlement phase of excitable focuses. Since the presently employed model allows for a precise regulation of the re-settlement time, exact results can be obtained already by fairly small system sizes, thus keeping the required computational resources minimal whilst still preserving main dynamical features.

Importantly, long refractory times characterise several biological oscillators. One of the most prominent examples are oscillations of free cytosolic calcium concentration that play an important role in regulating several cellular processes [30,31]. In response to cellular agonists acting on receptors in the cell membrane, calcium is rapidly released from intracellular stores such are for example the endoplasmic or sarcoplasmic reticulum. Thus, the mechanism regulating cytosolic calcium oscillations essentially acts as an excitable system, residing in a steady state near a bifurcation point to the oscillatory regime; however, during the time when intracellular stores are refilled, the system is non-excitable. Hence, only when the intracellular stores are full, the system regains excitability so that external agonists can evoke the next elevation of cytosolic calcium concentration.

In several tissues cellular oscillators are coupled via gap junctions through which calcium diffuses and regulates cell synchronisation. The spatiotemporal organisation of signal transduction in the tissue is hence determined by cellular oscillators possessing properties that are incorporated also in the presently studied system. The most crucial property is that real-life oscillators have a characteristic refractory time that determines the spatiotemporal behaviour at the tissue level.

There is a lack of experimental studies analysing spatiotemporal signal transduction at micro- and macro-scales because it is difficult to observe cellular end tissue events at the same time. Some very recent experiments have been made by laser scanning confocal microscopy. In airway and arteriole smooth muscle cells calcium oscillations have been observed in single cells that represent constitutive parts of a lung slice [32,33]. However, since airway smooth muscle cells are typical representatives of multi-unit muscles that are made up of weakly coupled and spatially non-organised cells, only asynchronous calcium oscillations have been observed. In the future, it would be interesting to investigate also spatially well-organised and strongly coupled cells, i.e. the so-called mono-unit systems, as are for example heart muscles or muscles in the gut.

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